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*Metania ovogemmata* sp. nov. and *Radiospongilla streptasteriformis* sp. nov. are figured and described. *M. ovogemmata* represents the first record of the genus *Metania* Gray in Australia and its discovery establishes a connection between the Australian and South American spongillid faunas. *R. streptasteriformis* extends the range of the genus *Radiospongilla* Penney and Racek in Australia and a study of its relationship to other members of the genus indicates that there has been a radiation of radiospongillids in Australia. *Eunapius sinensis* (Annandale), previously recorded from the eastern states of Australia, is recorded for the first time from the Northern Territory.

This new information forms the basis for further speculation on the origins and relationships of Australian spongillids.

J. Stanisic, Department of Malacology, The Australian Museum, P.O. Box A285, Sydney South, Australia 2000; manuscript received 16 November 1977, in revised form 18 September 1978.

## INTRODUCTION

Following the comprehensive revision of a worldwide collection of freshwater sponges by Penney and Racek (1968), Racek (1969) completely revised the freshwater sponges of Australia and produced keys to all the described species. However, Racek's conclusions regarding the origin, dispersal and distribution of the Australian spongillid fauna were based on only limited material from the remote areas of central and northern Australia. Apart from the single record of *Radiospongilla hispidula* Racek from Darwin and two specimens of *Radiospongilla philippinensis* (Annandale) from Derby (W.A.), the material treated by Racek (1969) came from localities in the eastern states.

The paucity of material from these remote areas is largely due to their inaccessibility to previous collectors. However, with the establishment of the Crocodile Research Facility at Maningrida in Arnhem Land (N.T.), the author was able to obtain a collection of spongillids from Australia's far north. Detailed taxonomic studies of this collection revealed the presence of two new species of spongillids and the first record of the genus *Metania* Gray from Australia.

The sponges described in this paper provide new information on the distribution of the Australian spongillid fauna. More importantly however, this new information enables a reassessment of the possible origin of some of Australia's freshwater sponges to be made.

The taxonomic and morphological terminology used here follows Penney and Racek (1968). Preparation of the material followed the outlines presented by Gee (1931).

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## TAXONOMY

Genus *Metania* Gray

*Metania* Gray, 1867, p. 551

*Metania* Penney and Racek, 1968, p. 147 (and synonymy)

*Type species: Spongilla reticulata* Bowerbank (1863)

This genus, as redefined by Penney and Racek (1968), includes those species which possess a single layer of radially arranged tubelliform gemmoscleres and free microscleres. The genus is restricted to tropical areas of Asia, Africa and South America. The new species, which is described below is the first representative recorded from Australia.

*Metania ovogemmata* sp. nov.

*Material:* Freshwater billabong ('Benamanarka Gunora') near Maningrida, Arnhem Land, Northern Territory, 12°00'S, 134°20'E, coll. G. Wells, 6. x. 76, holotype (Australian Museum Z3693).

*Description:* Sponge forming encrustations of variable thickness (1–3 mm) on logs in shallow water; surface reticulate and markedly hispid with spicules projecting through the dermal membrane. Skeleton consisting of tracts of spicules which form vague triangular meshes. Oscula conspicuous. Consistency of dry sponge firm.

Megascleres of two distinct size classes. The larger series forms the primary skeleton of the sponge, while the smaller series is mainly restricted to the vicinity of the gemmules, forming a spicular envelope around each gemmule. The larger series (Fig. 1 a-c) consists of stout fusiform amphioxea; slightly curved, ranging from smooth to incipiently spined except on the distal portions of the sclere. Length range 220–290  $\mu\text{m}$ , width range 10–20  $\mu\text{m}$ . Those in the smaller series (Fig. 1d,e) are short, stout, hastate amphioxea; curved and covered with numerous conical spines which tend to form whorl-like aggregations at the scleral apices. Length range 195–230  $\mu\text{m}$ , width range 12–20  $\mu\text{m}$ .

Microscleres (Fig. 1f,g) slender, fusiform amphioxea; straight to slightly curved and covered with numerous spines. In the central portion of the sclere these spines become longer and complex. Length range 60–90  $\mu\text{m}$  width range 2–4  $\mu\text{m}$ .

Gemmoscleres (Fig. 1h-1) tubelliform with an almost circular rotule at one end and terminating in a smooth knob at the other. The face of the rotule is clear of any striations while the margins are strongly recurved. The shaft of the sclere possesses a number of large conical spines. Length range 25–35  $\mu\text{m}$ , width of shaft 2–4  $\mu\text{m}$ , diameter of rotule 16–21  $\mu\text{m}$ , width of terminal knob 3–7  $\mu\text{m}$ .

Gemmules (Fig. 1m,n) large and oviform; abundant and scattered throughout the skeletal meshwork. The pneumatic layer of the gemmule is thin with the gemmoscleres embedded radially so that the terminal knob is to the outside. The knob does not project beyond the outer gemmular membrane. Surface of the gemmule is granular. The foramen of the gemmule is tubular and the porous tube projects a short distance beyond the outer gemmular membrane. The gemmules are surrounded by an envelope of spiny megascleres. Dimensions of gemmules 420–520  $\mu\text{m}$  (long axis) by 260–370  $\mu\text{m}$  (short axis).

*Type:* Holotype with slides and vial of gemmules in the Australian Museum.

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The presence of two classes of megascleres and the peculiar arrangement of the smaller series around the gemmule, suggest that this species is most closely related to *Metania reticulata* (Bowerbank) which occurs in the Amazon River of South

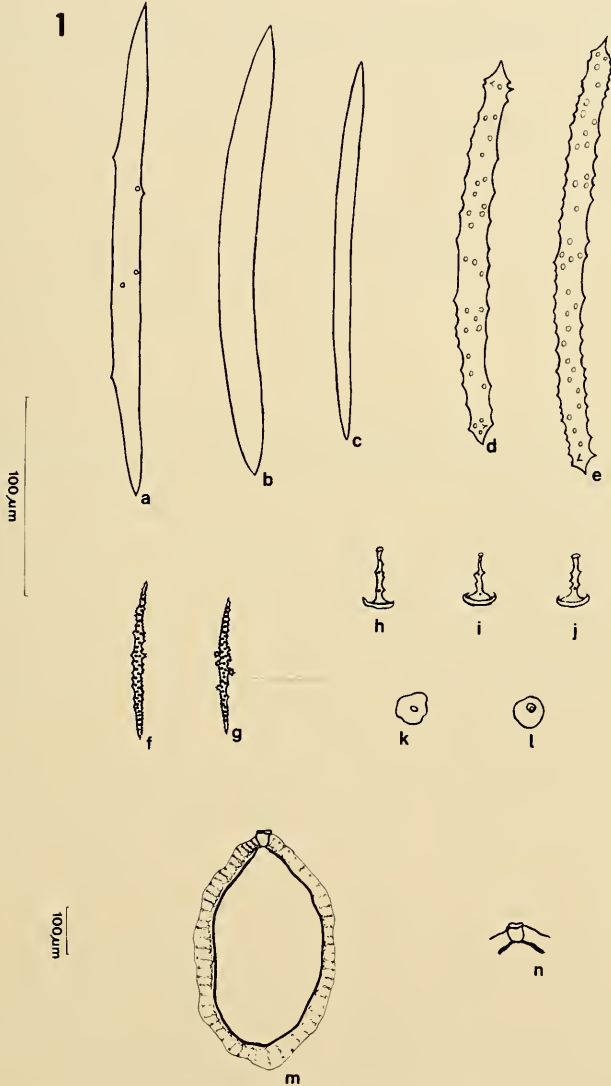


Fig. 1. *Metania ovogemmata* sp. nov.

a-c. larger series of megascleres  
 d-e. smaller series of megascleres  
 f-g. microscleres  
 h-j. gemmoscleres

k-l. rotules of gemmoscleres  
 m. gemmule  
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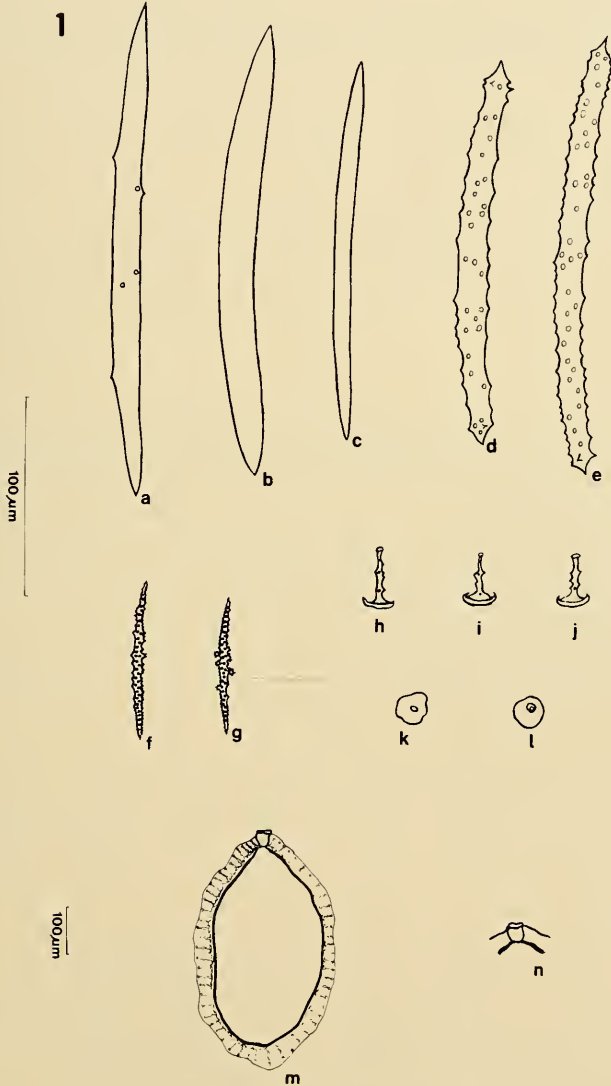


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America. However, the difference in the size of the megascleres of the two species and the fact that these are amphioxea in *M. ovogemmata* as opposed to amphistrongyla in *M. reticulata*, indicate that *M. ovogemmata* deserves separate specific status.

The striking arrangement of the hastate amphioxea in *M. ovogemmata* around the gemmule, appears to be an adaptation indicative of species which have small gemmoscleres and an associated small pneumatic layer in the gemmule. Similar capsules are found in *Trochospongilla* Vejdovsky, *Uruguaya* Carter and *Drulia* Gray, all of which have small radially arranged gemmoscleres and small pneumatic layers.

Considering the presence of the two congeners, *Metania vesparia* (von Martens) and *Metania vesparioides* (Annandale) in the Asian region, the relationship of *M. ovogemmata* to a South American species has important implications regarding the possible origin of this genus. These implications will be discussed later.

*Genus Radiospongilla* Penney and Racek

*Radiospongilla* Penney and Racek, 1968, p. 61 (and synonymy).

*Radiospongilla* Racek, 1969, p. 279.

*Type species: Spongilla sceptrioides* Haswell (1882).

Penney and Racek (1968) introduced this genus as a link between those spongillids with acerate gemmoscleres and those with birotulate gemmoscleres, showing that the previous grouping of the spongillids into the two sub-families Spongillinae and Meyeninae was unwarranted. Hitherto six species are known from Australia.

*Radiospongilla streptasteriformis* sp. nov.

*Material:* Freshwater billabong ('Benamanarka Gunora') near Maningrida, Arnhem Land, Northern Territory, 12°00'S, 134°20'E, coll. G. Wells, 6. x. 76, holotype (Australian Museum Z3695).

*Description:* Sponge forming very thin encrustations in the corrugations of bark from logs in shallow water. Surface of the sponge is an irregular network of spicules with some of these projecting through a poorly developed dermal membrane giving the sponge a slightly hispid appearance.

Megascleres (Fig. 2a,b) slender to stout, curved fusiform amphioxea; strongly spined over the entire length with no distinct aggregation of the spines. Length range 160–200  $\mu\text{m}$ , width range 4–10  $\mu\text{m}$ .

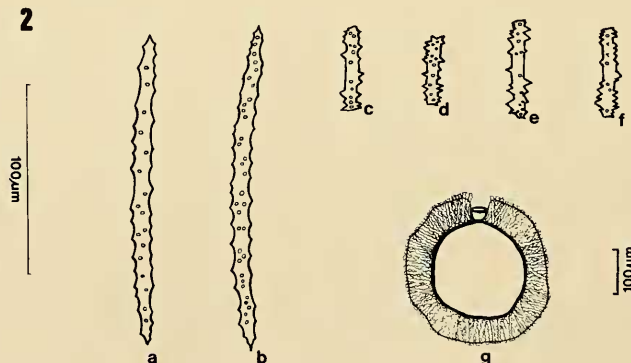


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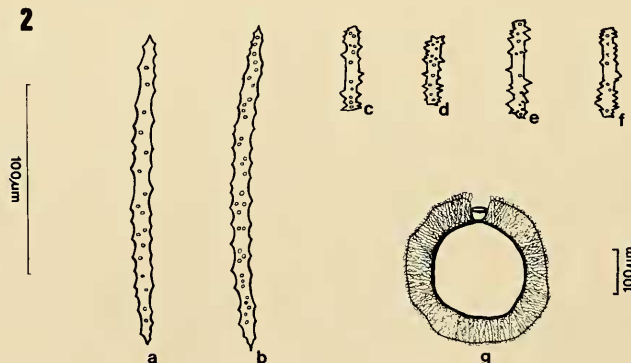


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- a-b. megascleres
- c-f. gemmoscleres
- g. gemmule



Microscleres absent.

Gemmoscleres (Fig. 2c-f) short, stout abrupt amphistrongyla covered with numerous long straight spines. Occasionally the central portion of the sclere is less spined than the distal portions. Straight to slightly curved. Length range 40–65  $\mu\text{m}$ , width range 4–6  $\mu\text{m}$ .

Gemmules (Fig. 2g) abundant and scattered throughout the symplasm of the sponge. These are large and spherical with a well developed pneumatic layer.

The gemmoscleres are embedded radially in the pneumatic layer and project beyond the outer gemmular membrane, making the surface of the gemmule distinctly hispid. The porus tube does not project beyond the outer gemmular membrane and is surrounded by a conical depression. Diameter of gemmule 340–440  $\mu\text{m}$ .

*Type*: Holotype with slides and vial of gemmules in the Australian Museum.

*Distribution*: Hitherto known only from the type locality in Arnhem Land, Northern Territory.

*Colour*: Not reliably recorded.

*Discussion*: The discovery of *Radiospongilla streptasteriformis* in the alkaline waters of Australia's north, suggests that the genus *Radiospongilla* Penney and Racek may not be as restricted in distribution as Racek (1969) indicated. Based largely on collections from the eastern seaboard, Racek suggested that most species of this genus preferred acidic waters.

The gemmoscleres of *R. streptasteriformis* which are small and evenly spined abrupt amphistrongyla, readily separate this species from its congeners. However, the dimensions of the megascleres and gemmoscleres indicate that this species is closely related to *Radiospongilla synoica* Racek and *Radiospongilla cantonensis* (Gee). These three spongillids are characterized within the radiospongillids by their small megascleres and small gemmoscleres. They show a range of gemmosclere structure from amphioxea (*R. synoica*) through abrupt amphistrongyla (*R. streptasteriformis*) to the formation of almost perfect pseudorotules (*R. cantonensis*).

As *R. synoica* is endemic to eastern Australia and *R. cantonensis* is also present in eastern Australia (unpublished data), the distribution of these three species indicates a localized radiation from the central stem of radiospongillids as represented by the extant species *Radiospongilla cerebellata* (Bowerbank) and *Radiospongilla philippinensis* (Annandale). The evolutionary importance of the genus *Radiospongilla* (Penney and Racek, 1968; Racek, 1969; Racek and Harrison, 1975), makes the occurrence of such a radiation in the Australian region assume particular relevance in discussions concerning the origins of spongillids. The significance of this point will be discussed later.

#### Genus *Eunapius* Gray

*Eunapius* Gray, 1867, p. 552

*Eunapius* Penney and Racek, 1968, p. 21 (and synonymy).

*Eunapius* Racek, 1969, p. 271

*Type species*: *Spongilla carteri* Bowerbank (1863)

This genus is characterized by species which have a tangential arrangement of gemmoscleres around the gemmule and which lack free microscleres. Members of the genus are widely distributed and four species are recorded from Australia. *Eunapius sinensis* (Annandale) is known from the eastern and western river systems in New South Wales and Queensland. It is here recorded for the first time from the Northern Territory.

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*Type*: Of *S. sinensis* in the collection of the United States National Museum.

*Distribution*: According to Penney and Racek (1968), ranging from USSR through Manchuria and mainland China to Australia. Not known from SE Asia.

*Discussion*: The characteristics of this specimen in both its mode of growth and spicular components make it fully comparable with the previously recorded Australian specimens. Racek (1969) considered that the thick pneumatic coat of the gemmule, which is reinforced by tangential layers of robust gemmoscleres, makes this species particularly suited to harsh environments.

The specimen was found growing in very close association with *M. ovogemmata*. However, the pavement layers of gemmules of *E. sinensis* were readily discernible from the more loosely scattered gemmules of *M. ovogemmata*.

## GENERAL DISCUSSION

*Origins and Relationships of the Australian Spongillids*

Racek (1969) believed that most of the Australian spongillids were a southern extension or represented mere races of the Asian fauna. He based this assessment on the distribution of the extant spongillids in these two areas. More recently however, Racek and Harrison (1975) have reconsidered this theory.

Racek and Harrison examined the phylogenetic position of the fossil spongillid *Palaeospongilla chubutensis* Ott and Volkheimer which was discovered in the lacustrine sediments of the Cretaceous of Argentina. Consideration was given to the southern distribution of a number of the extant spongillids which showed close affinity with the fossil. In particular, Racek and Harrison referred to the presence in Australia of members of the genus *Radiospongilla* Penney and Racek, which could be related to the Cretaceous fossil, and the distribution of *Spongilla alba* Carter in both Australia and South America. These workers considered the pattern of continental drift in an attempt to reconstruct dispersal routes leading from the Cretaceous fossil to the present day distribution of spongillid fauna.

Racek and Harrison concluded that it was more reasonable to consider that Asia and Australia had independent faunal gains along dispersal routes which existed prior to the dismemberment of the great southern continent Gondwanaland. Two dispersal routes leading west-east were suggested. One route was along the connected South American, Antarctic and Australian plates, while the other was through Africa and Indo-Pakistan. Subsequently there may have been interchange between the Asian and Australian faunas. However, the evidence for these conclusions was based almost solely on the assumption that the extant fauna was directly related to the Cretaceous fossil.

With the discovery of *Metania ovogemmata* sp. nov. in Australia, a reassessment of spongillid dispersal routes is possible. It has already been demonstrated that *M. ovogemmata* is more closely related to *Metania reticulata* (Bowerbank) of South America than to its Asian congeners. The affinity between these extant spongillids can only be reasonably explained by divergence from a common stock. In order to account for the present distribution of these two species, subsequent dispersal would have required connected land masses which were present during the Mesozoic when Australia and South America were part of Gondwanaland (Smith, 1971).

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The specimen was found growing in very close association with *M. ovogemmata*. However, the pavement layers of gemmules of *E. sinensis* were readily discernible from the more loosely scattered gemmules of *M. ovogemmata*.

## GENERAL DISCUSSION

*Origins and Relationships of the Australian Spongillids*

Racek (1969) believed that most of the Australian spongillids were a southern extension or represented mere races of the Asian fauna. He based this assessment on the distribution of the extant spongillids in these two areas. More recently however, Racek and Harrison (1975) have reconsidered this theory.

Racek and Harrison examined the phylogenetic position of the fossil spongillid *Palaeospongilla chubutensis* Ott and Volkheimer which was discovered in the lacustrine sediments of the Cretaceous of Argentina. Consideration was given to the southern distribution of a number of the extant spongillids which showed close affinity with the fossil. In particular, Racek and Harrison referred to the presence in Australia of members of the genus *Radiospongilla* Penney and Racek, which could be related to the Cretaceous fossil, and the distribution of *Spongilla alba* Carter in both Australia and South America. These workers considered the pattern of continental drift in an attempt to reconstruct dispersal routes leading from the Cretaceous fossil to the present day distribution of spongillid fauna.

Racek and Harrison concluded that it was more reasonable to consider that Asia and Australia had independent faunal gains along dispersal routes which existed prior to the dismemberment of the great southern continent Gondwanaland. Two dispersal routes leading west-east were suggested. One route was along the connected South American, Antarctic and Australian plates, while the other was through Africa and Indo-Pakistan. Subsequently there may have been interchange between the Asian and Australian faunas. However, the evidence for these conclusions was based almost solely on the assumption that the extant fauna was directly related to the Cretaceous fossil.

With the discovery of *Metania ovogemmata* sp. nov. in Australia, a reassessment of spongillid dispersal routes is possible. It has already been demonstrated that *M. ovogemmata* is more closely related to *Metania reticulata* (Bowerbank) of South America than to its Asian congeners. The affinity between these extant spongillids can only be reasonably explained by divergence from a common stock. In order to account for the present distribution of these two species, subsequent dispersal would have required connected land masses which were present during the Mesozoic when Australia and South America were part of Gondwanaland (Smith, 1971).

Although Racek and Harrison (1975) came to similar conclusions regarding the importance of Gondwanaland in spongillid dispersal they considered only dispersal routes which were west-east along the Mesozoic continuity. A study of the distribution of the genus *Metania* Gray reveals the possibility of dispersal in an east-west direction. *Metania vesparia* (von Martens) and *Metania vesparioides* (Annandale) which occur through Africa, Burma, Borneo and Indonesia indicate dispersal and speciation from South America to Africa and Indo-Pakistan. As *M. ovogemmata* possesses a number of ancestral traits, e.g. two classes of amphioxeous megascleres, it is possible to demonstrate an evolutionary series from *M. ovogemmata* through *M. reticulata* to the Asian congeners. Therefore, in this case dispersal and speciation has most probably occurred in an east-west direction with the genus *Metania* having its origins in the Australian region.

Although little is known of the origin of the spongillids with birotulate gemmoscleres (e.g. *Metania*), they are considered to have arisen from an hypothetical stock from which the extant genus *Radiospongilla* Penney and Racek has also been derived (Penney and Racek, 1968). The gemmoscleres of *Radiospongilla cantonensis* (Gee) and *Radiospongilla crateriformis* (Potts) possess almost perfect rotules, suggesting that these two species share a common ancestry with the birotulate genera. In order to demonstrate more conclusively the emergence of birotulate genera in Australia, it is necessary to consider the distribution of radiospongillids which are considered to be phylogenetically related to these genera. However, this requires a reassessment of the suggested relationships within the genus *Radiospongilla*.

Penney and Racek (1968) considered that *R. cantonensis* and *R. crateriformis* form part of an evolutionary line within the radiospongillids. Their conclusions were based on the fact that the gemmoscleres of both these species possessed pseudorotules. This view implies that the birotulate genera have had a monophyletic origin. Such a view, however, does not explain the marked morphological diversity of the birotulate genera. Moreover, this view leads to difficulties in explaining relationships between the distribution of these radiospongillids and the distribution of the birotulate genera.

Recent developments based on the work of Poirrier (1974, 1976) and Stanisic (1977) enable an alternative view to be put forward. These workers have shown that using gemmoscleral form as a first principle for establishing relationships within genera, is not entirely valid. Such features are subject to ecomorphic variation which can mask true relationships. If, on the other hand one considers the length of the megasclere as a basis for assessing relationships, a new and more reasonable argument presents itself.

The difference in the lengths of the megascleres of *R. cantonensis* and *R. crateriformis* indicates that these two species have diverged from the central line of the radiospongillids at different times. The central line is represented by the *Radiospongilla cerebellata* (Bowerbank) group. Hence it is possible that the birotulate genera have arisen from more than one ancestor and that their origins are polyphyletic. Using megasclere length as a criterion, it is now also reasonable to suggest that *R. cantonensis* is more closely related to *Radiospongilla synoica* Racek and *Radiospongilla streptasteriformis* sp. nov. as all three spongillids have small megascleres. In view of the fact that these three spongillids occur almost solely in the Australian region, it is probable that they represent a radiation from a common ancestor in this region. Therefore, if *R. cantonensis* shares a common ancestry with some of the birotulate genera in Australia it is possible to document the emergence of birotulate genera in Australia. This not only supports the views of the present study regarding the origins of the genus *Metania* but also the view of Racek (1969), who considered that *Heterorotula* Penney and Racek evolved in Australia.

Although Racek and Harrison (1975) came to similar conclusions regarding the importance of Gondwanaland in spongillid dispersal they considered only dispersal routes which were west-east along the Mesozoic continuity. A study of the distribution of the genus *Metania* Gray reveals the possibility of dispersal in an east-west direction. *Metania vesparia* (von Martens) and *Metania vesparioides* (Annandale) which occur through Africa, Burma, Borneo and Indonesia indicate dispersal and speciation from South America to Africa and Indo-Pakistan. As *M. ovogemmata* possesses a number of ancestral traits, e.g. two classes of amphioxeous megascleres, it is possible to demonstrate an evolutionary series from *M. ovogemmata* through *M. reticulata* to the Asian congeners. Therefore, in this case dispersal and speciation has most probably occurred in an east-west direction with the genus *Metania* having its origins in the Australian region.

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Inter-generic relationships within the family Spongillidae still need to be reliably established. The broad hypothesis regarding the relationship of the genus *Radiospongilla* to the birotulate genera which was put forward by Penney and Racek (1968), while providing some insight, is too vague to provide the explanatory and predictive powers which would make such a hypothesis useful in determining relationships. On the other hand, the specific arguments which have been presented above, can be used to demonstrate the emergence of birotulate genera in Australia. It is now also possible to predict a relationship between the radiospongillids mentioned above and these birotulate genera. Although highly speculative, such a hypothesis is favoured by the fact that its restrictive nature makes it open to testing by future research and discoveries.

As mentioned at the beginning of the discussion, the origins and affinities of the Australian freshwater sponges have been discussed by Racek (1969) and Racek and Harrison (1975). The new material documented in the present study, has enabled a further assessment to be made of the considerations initiated by these workers and it is now possible to show a definite connection with the unique South American spongillid fauna. Reconsideration of inter-generic relationships and distribution patterns indicate the possibility of an Australian origin for some of the birotulate genera, in particular *Metania*. The information provided by this new material however, emphasizes the need for further collecting within the Australian region.

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